

The Bivalvia: Future directions for research

Brian Morton

Department of Zoology and The Swire Marine Laboratory, The University of Hong Kong, Hong Kong

The theme of this paper and attendant symposium is "Future Research Directions for the Bivalvia". This paper presents a personal view about a class of animals for which we share a common interest and enthusiasm.

My involvement with the Bivalvia goes back many years when I first began researches upon *Dreissena polymorpha* (Pallas), then and now a continuing problem in the exploitation of fresh waters in Europe. I left *Dreissena* in 1969, when I completed my Ph.D. and, at the same time, left Great Britain to take up a teaching post in Hong Kong. I believed I had left *Dreissena* for ever. Just this year, however, I have been asked to write the introductory chapter for a book on *Dreissena*, the stimulus for publishing such a volume being the introduction of this species into North America via the Great Lakes and the economic consequences of the introduction that are already being felt. I will return to the general topic of introductions later, but it is worth noting, in passing, that the Bivalvia, despite their sedentary habits, do have a tendency to travel to the most unlikely places.

I was a student of Professor R. D. Purchon who was, in turn, a student of the late Sir Maurice Yonge, arguably the father of modern research upon the Recent Bivalvia. I first met Maurice in 1967 when he visited the University of London to talk to the student Biology Society of which I was Secretary. He and I, of course, discussed *Dreissena* for he was working on it too and so a friendship was founded that lasted for 20 years until his death in 1986. I was responsible for organizing a symposium on the Bivalvia in his honour but which was, in the event, in his memory, at the IX Malacological Congress in Edinburgh in 1986. He died just a few months before the meeting was convened. The Proceedings of that Symposium were subsequently published in 1990 (Morton, 1990a).

Maurice and his students of the Bivalvia, for example, G. Owen, J. A. Allen, T. H. J. Gilmour, R. G. B. Reid, A. D. Ansell and R. D. Purchon, have had a powerful impact upon not only our understanding of the Recent representatives of this class, but also upon the Mollusca and Zoology in general for much of this century, notably in Great Britain. Some of these students have emigrated to Canada

and the U.S.A., for example, where their influence, and thus Maurice's, persists. North America too has fostered endemically students of the Bivalvia through such eminent scientists as K. M. Wilbur, R. D. Turner, S. M. Stanley, M. R. Carriker, K. J. Boss, J. Pojeta and N. D. Newell, not forgetting such legendary characters as W. H. Dall, W. R. Coe, T. C. Nelson and V. L. Loosanoff. This is not, however, going to be a discussion about famous bivalve malacologists and you have to forgive me if I have not mentioned your name or that of a mentor you think significant and comparable with those just identified. I am similarly not ignoring equally famous bivalve malacologists from, for example, Europe (V. Scarlato), Australia (B. Runnegar) and elsewhere: the only point I am trying to make is that there are rich geneologies of eminent zoologists who have made the Bivalvia their own and stamped their mark upon a group that today is close to serving as a classic model of adaptive radiation. Some of our most eminent zoologists are students of the Bivalvia. The class is of importance and interest.

With this in mind, I looked back over the last twenty-five years of *The Journal of Molluscan Studies*, so renamed after 1976 from its official status as the *Proceedings of the Malacological Society of London*, one of malacology's most prestigious societies and which, in 1993, will celebrate its centenary. I counted the number of papers published in each volume, their page length and noted which of them were concerned with the Bivalvia. The results of this simple analysis are shown in figure 1 wherein it can be seen that (A), the number of papers published annually has increased (the quantum jump in 1982 results from the initiation of the publication of Research Notes) although (B), page length, has decreased somewhat (the decline in 1982 again results from the initiation of the publication of Research Notes). Look, however, at figure 1C. The number of papers published on the Bivalvia since a heyday in 1967, when 67% of the papers were on this class, has declined progressively. So, I suspect, has the variance. In the 1960's and 1970's, volumes would contain between 25% and 45% information on the Bivalvia. In the 1980's such figures were between 10% and 25%. In 1990, the figure is approximately 10%. Extrapolating

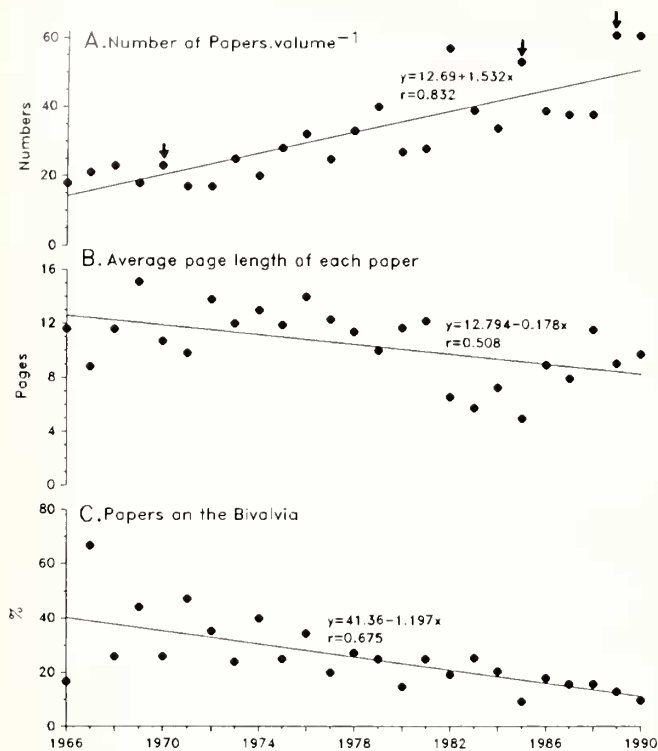


Fig. 1. A, Numbers of papers; B, average page length of each paper; C, % numbers of papers on the Bivalvia published in *Journal of Molluscan Studies* (1967-1990).

such a graph, I have concluded that *The Journal of Molluscan Studies* will cease to publish papers on the Bivalvia by about the time the parent society celebrates its centenary. I have been invited to give the plenary lecture on the Bivalvia at the Conference to celebrate the Society's centennial: it rather looks as though I will be talking to myself! The editors of the *Journal* over these years have been N. B. Eales, A. Graham and J. D. Taylor, all gastropod workers, but I am not suggesting uncharitably that they are responsible for this decline. Rather, it appears that there is a declining interest in this class of the Mollusca, at least in Great Britain.

I have also taken an American malacological journal, *Veliger*, appropriate because of its affiliation to the California Malacozoological Society, and performed the same analysis of the published papers. Here, a similar trend is apparent with regard to the numbers of papers being published (Fig. 2A) although their average length (Fig. 2B) is increasing, unlike papers in the *Journal of Molluscan Studies*. So, too, however (Fig. 2C), is the incidence of papers on the Bivalvia, again in contrast to the *Journal of Molluscan Studies*.

We thus see a fundamental difference in trends with respect to the Bivalvia in the British and American journals. I do not, however, wish to make too much of this, after all there are dozens of malacological journals and an analysis

of them all would be needed to obtain a clearer picture. I will make one point, however. The loss to North America of some of C. M. Yonge's students, for example, R. G. B. Reid, T. H. J. Gilmour, W. D. Russell-Hunter and P. V. Fankboner, and their potential to, in turn, engender students of the Bivalvia can help us to explain the decline in British studies of the Bivalvia and the increase in North American. Scientific emigration from Britain has been going on for decades and is a damning indictment of British Government policy with regard to its science and its scientists. But is there a wider trend with regard to research upon the Bivalvia?

With the help of my colleague, Professor J. Britton, I have conducted a library search of BIOSIS for the numbers of papers published on the Mollusca, Bivalvia, Gastropoda and Cephalopoda since 1969, i.e. the last 22 years. Numbers of papers published on the Mollusca have, as might be anticipated, increased from 379 in 1969 to 801 in 1990, i.e. an overall increase of 422 or 113.5% (Table 1). Numbers of papers on the Cephalopoda, Gastropoda and Bivalvia have increased by 13 (11.9%), 232 (128.9%) and 177 (135.1%), respectively. The largest overall percentage increase is, thus, upon the Bivalvia. Looking at publications upon the three classes in terms of their percentage contribution to the molluscan body of literature (Fig. 3), trends become apparent. The relative number of papers published on the Cephalopoda has declined, since 1969, by as much as ~ 50%. Research on the Gastropoda seemed to peak in about 1972, corresponding with a trough in publications on the Bivalvia.

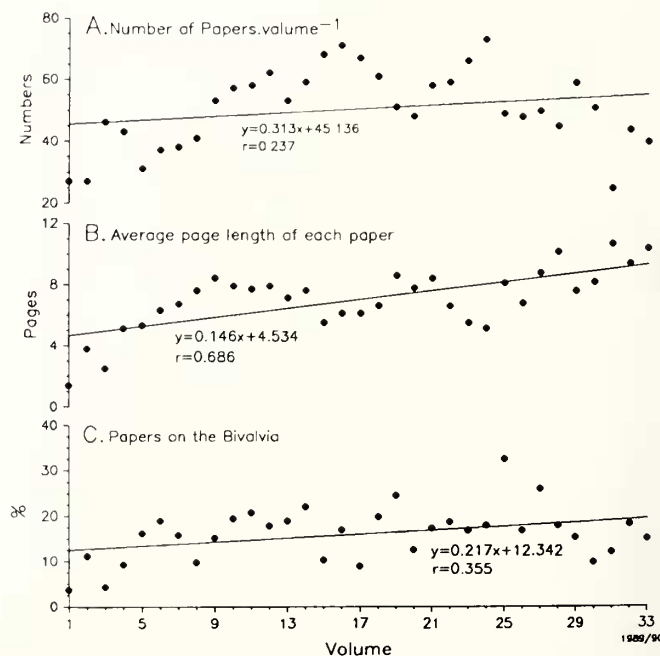


Fig. 2. A, Number of papers; B, average page length of each paper; C, % numbers of papers on the Bivalvia published in *Veliger* (1967-1990).

Table 1. Numbers of papers published on the Mollusca and the three largest classes (plus percentages) between 1969 and 1990 (BIOSIS data).

	Mollusca		Gastropoda		Cephalopoda		Bivalvia	
	No.	%	No.	%	No.	%	No.	%
1969	379		180	47.5	68	17.9	131	34.6
1970	359		185	51.5	68	18.9	106	29.5
1971	459		250	54.5	68	14.8	141	30.7
1972	524		296	56.6	68	13.0	160	30.5
1973	511		272	53.2	68	13.3	171	33.5
1974	561		270	48.1	68	12.1	223	39.8
1975	669		315	47.1	86	12.8	268	40.1
1976	716		353	49.3	88	12.3	275	38.4
1977	728		355	48.8	88	12.1	285	39.1
1978	717		323	45.0	88	12.3	306	42.7
1979	708		355	50.1	88	12.4	265	37.4
1980	747		357	47.8	92	12.3	298	39.9
1981	829		396	47.8	92	11.1	341	41.1
1982	811		375	46.2	92	11.3	344	42.4
1983	686		325	47.4	92	13.4	269	39.2
1984	833		376	45.1	92	11.0	365	43.8
1985	856		428	50.0	93	10.9	335	39.1
1986	843		422	50.0	81	9.6	340	40.3
1987	880		425	48.3	81	9.2	374	42.5
1988	930		453	48.7	82	8.8	395	42.5
1989	944		453	48.0	81	8.6	410	43.4
1990	801		412	51.4	81	10.1	308	38.5

Since 1974 the percentage contribution of papers on the Gastropoda to the body of molluscan literature has remained relatively stable between 45% and 50%. Since the early 1970's, however, publications on the Bivalvia have increased from around 30% to achieve virtual parity with the Gastropoda at between 40-45%. Thus, the global relative significance of the Bivalvia to working scientists has increased. Relatively more papers are being published on the Bivalvia today, than upon any other molluscan class. Again, I do not wish to make too much of these figures, after all BIOSIS is not comprehensive, but it may be making you think about the remarks made earlier concerning the British and American malacological journals. Do such figures match up

with those obtained from the *Journal of Molluscan Studies* and *The Veliger*? The short answer is that they do not and we thus see that our 'academic' malacological journals are not reflecting, in their contents, the full extent of the research currently being undertaken on the Bivalvia.

I now wish to change the direction and introduce this Symposium but, also, to highlight some areas where I believe more research upon the Bivalvia is needed. I will, however, return to the above figures and arrive at a general conclusion.

The Bivalvia are an ancient group having their origins in the Palaeozoic. *Fordilla* and *Pojetia* are considered to be the oldest bivalves but yet, as Pojeta and Runnegar (1976) point out, we still have not reconstructed an adequate working picture of how such an animal was organized in its shell (Fig. 4). Since the Palaeozoic, the class has radiated, leaving a rich series of fossils and thus a good fossil history that enabled Newell (1965) to lay the basis for a sound, workable, system of classification that, with subsequent minor amendments, serves as a solid base for our understanding of the group's adaptive radiation. A symposium convened in 1977, organized by C. M. Yonge and T. E. Thompson (1978), under the auspices of The Royal Society, attempted, successfully, to marry the works of bivalve palaeontologists and Recent anatomists and we see arising from this venture a much greater appreciation of the need for the two groups of scientists to work together. In this symposium we explore such subjects further in the Evolution and Systematics Session but

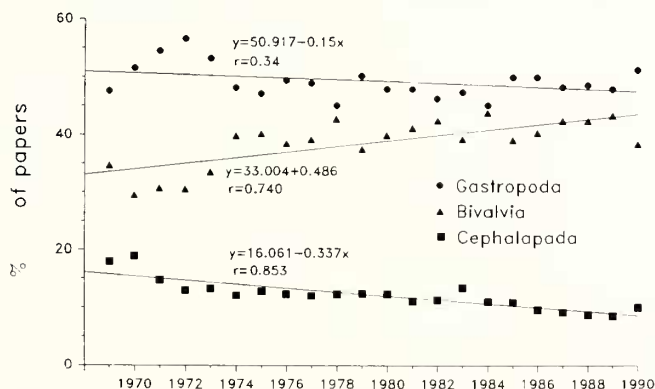


Fig. 3. Relative numbers of papers published annually on the Gastropoda, Bivalvia and Cephalopoda (BIOSIS data: 1969-1990).

there is, nevertheless, still much scope for closer co-operation between the two groups of scientists.

The researches of Stanley (1986a, b) and Vermeij (1989a, b) among others, have examined the rich *repertoire* of bivalve fossils to present ideas on the causes of marine extinctions and thereby explaining the past and present pat-

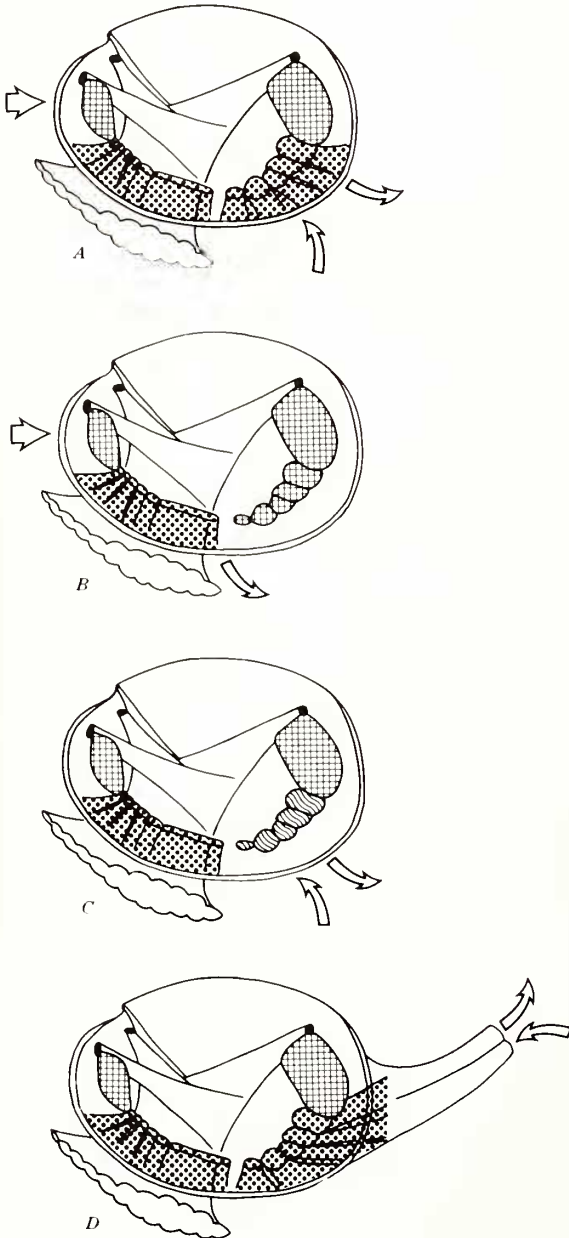


Fig. 4. Four possible explanations of the shell muscle insertions of the Early Cambrian pelecypod *Fordilla*. Adductor muscles are cross hatched; radial pallial muscles are stippled; muscles extending from the shell to the inner surface of the mantle are diagonally shaded; pedal muscle insertions are black. Arrows indicate possible water flow in and out of the mantle cavity. Note that if B were correct, the whole of the posterior end of the shell would be effectively sealed (after Pojeta and Runnegar, 1976).

terns of geographical restriction. We discuss bivalve biogeography in this Symposium in the Biogeography/Evolution Session. Anatomical studies on the Bivalvia, particularly Recent representatives of what are considered to be ancient lineages, are, however, still needed to help us understand more fully how the Bivalvia has managed to achieve the overall success it so richly, and clearly, enjoys. More importantly, however, such studies would help us to understand the anatomy of the rich array of fossil lineages without Recent representatives. Recently, Purchon (1987) suggested how grades of organization evolved within the Bivalvia to link lineage with lineage, so allowing us to better visualize its evolution. We know much about the shell and ligament structure, mantle fusions and gill, palp and stomach structure of many bivalve families. With continuing expansion and refinement, such information should allow us to make much more intelligent guesses at fossil body structure and cladistics could be a useful tool in this respect.

The adaptive radiation of the Bivalvia, boosted by a new era of success in the Mesozoic, continues to the present day (Stanley, 1977) and Vermeij (1977) and Taylor (1981) have suggested that such a diversification can be correlated with a 'Mesozoic Revolution' involving the adaptive radiation of a new suite of ecologically important predators that exploited the Bivalvia as a major source of food (Fig. 5). Such predation pressure was, thus, deeply felt by the bivalves, effectively driving them underground (Stanley, 1977) with concomitant adaptations for deep burrowing. It could also have fostered the exploitation of rocky shores by more modern heteromyarian heterodonts and the evolution of a coral host/bivalve borer symbiosis and modifications to the borer's shell in tropical species (Fig. 6) (Morton, 1990b). The independent appearance of cementation in many clades of bivalves

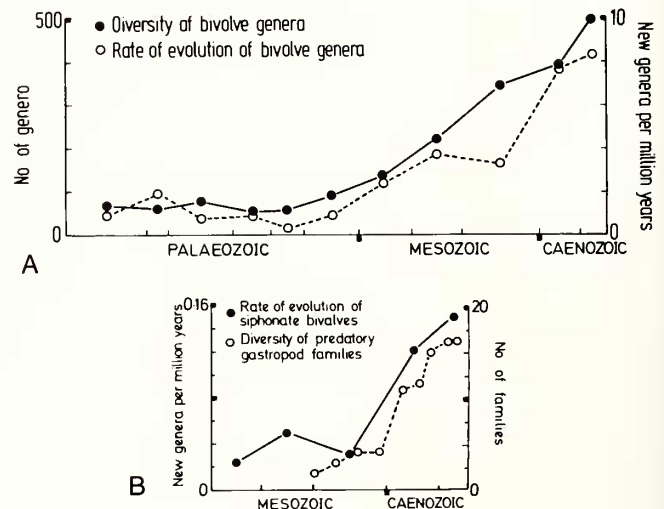


Fig. 5. A, rates of bivalve evolution at the family and generic levels (after Stanley, 1973); B, rates of bivalve and predatory neogastropod evolution at the family level during the Cenozoic (after Taylor, 1981).

in the Palaeozoic and Mesozoic can also be linked to predation pressure (Harper, 1991). Patterns of evolution in the Bivalvia are beginning to emerge.

Additional evidence, however, points to the success of the Bivalvia and to their importance in aquatic ecosystems. Sanchez-Salazar *et al.* (1987a, b) have shown how on a small sandy beach in North Wales, Great Britain, the cockle *Cerastoderma edule* Linné, is a far more important prey item for foraging crabs [*Carcinus maenas* (Linné)] and Oyster-catchers (*Haematopus ostralegus* Linné) than was conceived of previously. On this one small hectare bay, some 18 million juvenile cockles are consumed annually by these predators. Griffiths (1990) has suggested that the same pressures could be acting upon the gregarious bivalves of rocky shores and we can identify a wide range of mesogastropod, neogastropod and opisthobranch snails (*Natica*; *Melongena*, *Buccinum*, *Philine*), crabs (*Carcinus*; *Thalamita*), fish (*Pleuronectes*) and birds (*Haematopus*; *Crocethia*) that exploit bivalves as food. I believe bivalves to be much more important as primary consumers and prey in aquatic food chains than presently appreciated. This could already be recognized, but literature on the subject is published in non-malacological journals (just as with the above papers) such that they become mere names and numbers in papers dealing not so much with the animals themselves but with their presence or absence in communities. In studies of benthic assemblages, they have thus become relegated to a statistic.

I have pointed out (Morton, 1991b) that the Mesozoic Revolution also affected the Bivalvia in other ways, driving some of them into the deep seas where many still retain primitive characters and could thus constitute living fossils. I suggested, for example, that *Bathyarca* could be a living cryptodont (Morton, 1982) while Allen and Sanders (1969) have suggested that *Nucinella* is a living actinodont. Waller (1971) has suggested that the Propeamussidae are similarly primitive. The deep seas have, however, also fostered the evolution of remarkable structures that have enabled some lineages to pursue predatory careers. I refer of course to the septibranch Anomalodesmata studied by Yonge (1928), Allen (1983), Knudsen (1979), and Reid and Reid (1974) and leading me to suggest (Morton, 1991b) that, in this environment, **they** have become the agents for natural selection rather than a consequence of it. But, how much, in reality do we know of the lifestyle of such animals? If I were to suggest that a group of modern ungulates possessed representatives that are sedentary, ambushing, carnivores residing upon the Himalayas, think of the thousands of researchers who would desperately seek to find them. The mythical Yeti is a case in point. Why not for the septibranchs too then? For that is what they are, in essence, and urgently call out for greater study as very few of them have been studied alive.

There is, I thus believe, still much opportunity for significant research upon the evolution and adaptive radia-

tion of the Bivalvia.

Bivalves are also important economically. The gregarious shallow water representatives of the Pterioda and Heterodonta are two major lineages of bivalves that not only predators exploit as a major class of prey, but which also command our attention as food. Such animals as clams, cockles, mussels, oysters and scallops have been exploited as a human food resource since the Neolithic. Their importance is recognized in their contribution to the composition of the kitchen middens of such early people. Their importance continues today and many are now the subjects of thriving mariculture industries as reflected in the Food and Agriculture Organization (1989) figures for 1987 as presented in Table 2. Such data are, however, in reality, only the tip of a vast underwater iceberg of what the Bivalvia really constitute as a human food resource and their exploitation has led to a massive literature, often un-referred to by malacologists.

In today's 'economic' world I believe that academic malacologists must surely aim for an enhanced co-operation with mariculturists. We are aware of the researches and mariculture efforts of workers upon the oysters that have, through *Crassostrea gigas* (Ventilla, 1984), revitalized dying industries based upon less hardy species and of the overwhelming success of the Japanese scallop (Ventilla, 1982) and pearl oyster industries, but is there any significant research being undertaken on the wider range of other potentially cultivatable bivalves? One example of such a success has been the effort to re-establish overexploited and thus endangered

Table 2. Fishery statistics for the Mollusca - 1987. (After: Food and Agriculture Organization of the United Nations, 1989).

Commodity	Production (metric tonnes)
Abalone meat (frozen)	1,634
Snails (frozen)	3,964
Oyster meat (frozen)	2,974
Mussel meat (frozen)	11,242
Scallop meat (frozen)	38,866
Clams, cockles etc., meat (frozen)	66,634
Cuttlefish (frozen)	37,831
Squids (frozen)	563,720
Octopus (frozen)	53,183
General cephalopods (frozen)	158,092
General molluscs (frozen)	127,194
Oysters (dried)	3,934
Cuttlefish (dried)	242
Squids (dried)	48,431
Octopus (dried)	80
Squids (smoked)	5,684
General cephalopods (dried, salted, etc.)	15,431
General molluscs (dried, salted, etc.)	8,640
	Total
	1,147,776
	Bivalvia (Total)
	123,650

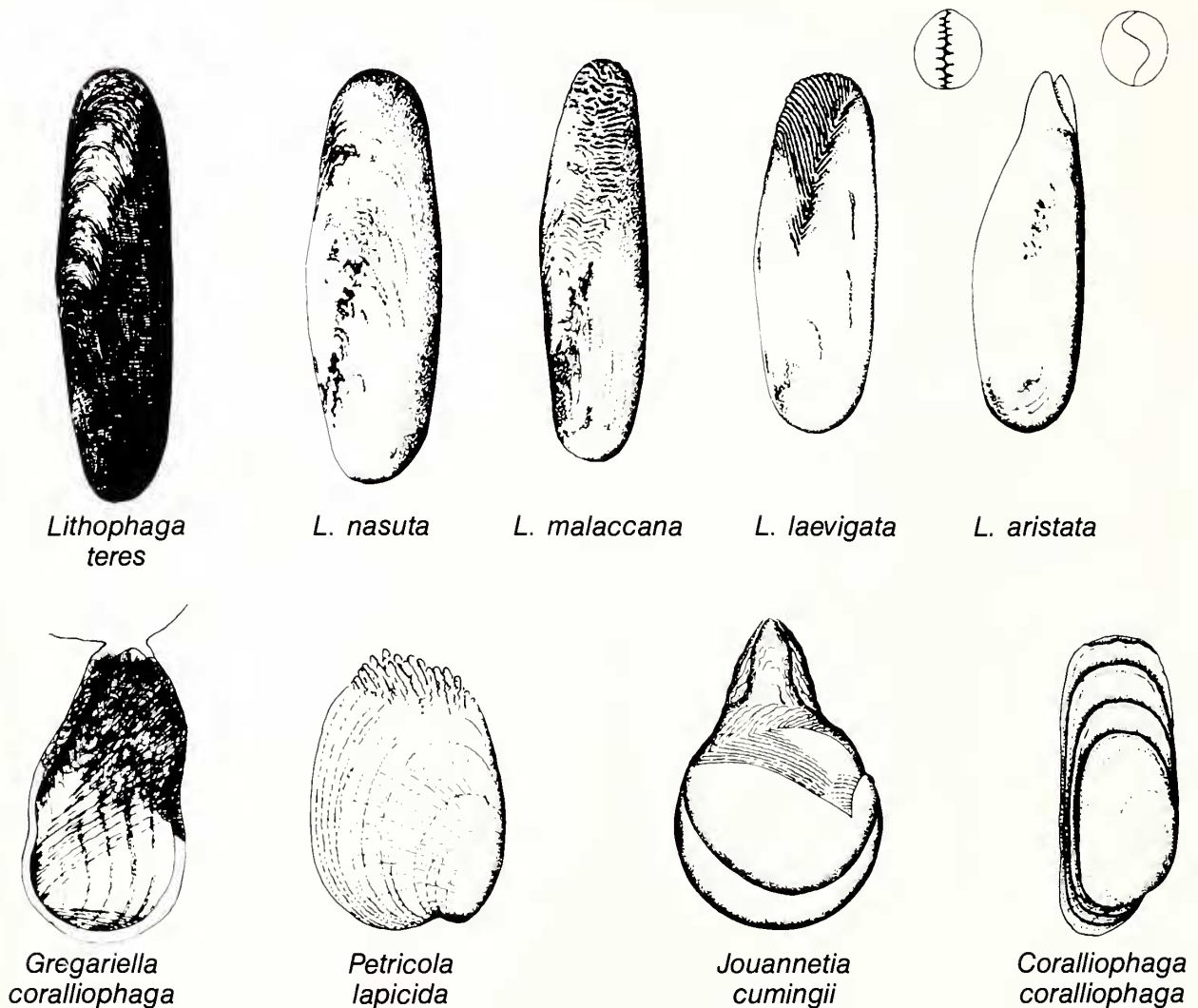


Fig. 6. Lateral views of the shells of coral boring and nesting bivalves. Also illustrated are end-on views of the posterior valve margins of *L. laevigata* and *L. aristata* (after Morton, 1991a).

Pacific island stocks of giant clams. Induced breeding has led not only to the probability of their conservations but also to the commercial development of them as a fishery resource, all the more significant because they do not have to be fed! Bivalves are economically important in other ways: as borers of wood, stone and plastic in the sea, so eloquently evaluated by R. D. Turner and her Harvard school. But, apart from this group, how many others are researching this economically important and fascinating group of bivalves?

We also are aware of the importance of mussels (and oysters) in the monitoring of an almost globally declining in-shore aquatic environment. Their propensity to acquire large amounts of sewage bacteria, red tide toxins and a suite of trace metals and organochlorines, may have reduced the importance of the Bivalvia in the public's eye as potential food (in

the absence of widescale depuration technology) but they are, nevertheless, virtually ideal indicators of environmental stress (Akberali and Trueman, 1985). In polluted Hong Kong, we have identified *Perna viridis* (Linné) (Mytilidae) (Lee, 1985), and, most recently, *Tapes philippinarum* (A. Adams and Reeve) (Veneridae) as highly resistant final indicators of sewage pollution. As such, they dominate polluted hard and soft shores, respectively, adding new significance to the ecological importance of the Bivalvia in such habitats but also posing the question: why is it that we have not exploited such a protein-producing potential for our own benefit? Such animals are also important, in today's polluted world, as good monitoring sentinels of ambient pollution loadings - but how many such 'mussel watch' networks have been developed, despite their repeated advocacy (National Academy

of Sciences, 1980). I have also to ask why it is that such research, when undertaken, is published not in malacological journals but in their more applied competitors, for example, *Aquaculture* and *Marine Pollution Bulletin*. Academic malacologists seem to have a mental block about the significance of research on the applied aspects of their subject and bivalve workers seem particularly aloof to such work.

Some 'opportunistic' bivalves too are important fouling agents, particularly in fresh waters. I earlier mentioned the subject of my first researches, *Dreissena polymorpha*, spread from its home base in the Caspian Sea throughout Europe during the 19th century Industrial Revolution and on into Great Britain. In 1989 it was introduced into the Great Lakes and, if there are any lessons to be learnt from history, it will invade progressively most of the Americas. The economic consequences of its spread will be enormous and yet I have to ask the question: how many reputable bivalve malacologists have stepped in to research it? My impression is few and, if true, then the story of *Dreissena*, as with *Corbicula flumina* (Müller) and its introduction into North America and subsequent spread (McMahon, 1983), will be left in the hands of engineers and aquatic ecologists whose relationship with the academic malacological fraternity who should be at the forefront of such research, is, at best, tenuous. Regretably, *Dreissena* and *Corbicula* were not discussed at this Symposium, nor even this Conference. Dare I suggest it, but modern bivalve researchers could do no better than to study *Dreissena* and *Corbicula* for they are what we need: living proof of the importance of the Bivalvia and which no gastropod, save vectors of schistosomiasis, can even remotely approach in terms of economic significance. There are many other examples of exotic introductions: *Mytilopsis sallei* Récluz introduced into the Pacific from the Atlantic (Morton, 1987a) and *Musculista senhousia* (Benson) introduced into the southern from the northern Pacific (Willan, 1987). With Pacific trade now outstripping that across the Atlantic, there will be many more such voyages by the Bivalvia (Carlton, 1987). It seems to me that bivalve workers must dirty their hands with such animals that appear, superficially, to be so uninspiring, because, in reality, it is these that are so clearly the visible proof of the success of the Bivalvia in our modern world.

My close friend and colleague, J. C. Britton, and I have, over the years, researched *Corbicula fluminea* here in America and elsewhere. Though others continue to argue with us (and I have no problem with that: arguments lost, won and then lost again are the stuff of science), we believe that only one species has been introduced but that it is polymorphic in terms of shell form, texture and colour and, most fascinating of all, sexual expression (Britton and Morton, 1986). We believe we are essentially seeing, through genotypic and phenotypic plasticity, evolution in action and yet how many other bivalve workers are actively engaged in sorting

out this riddle? Open up any volume of the *Biological Journal of the Linnean Society of London* to see the extent of the literature on polymorphism in the Gastropoda. My own paper on polymorphism in Hong Kong *Corbicula* (Morton, 1987b) was dismissed by a reviewer as wrong - there are simply two species involved - revealing the extent of one of our peers knowledge on this subject in the Bivalvia. I should add that a subsequent paper by Tsoi *et al.* (1990) has demonstrated that there is no significant allozyme difference between the two morphs while Kijviriya *et al.* (1991) have shown, using the same electrophoretic approach, that 21 nominal species of *Corbicula* in Thailand are all assignable to *C. fluminea*. Cain (1988) has recently published a paper on polymorphism in deep-burrowing *Macoma balthica* (Linneé) and suggests that it results from apostatic selection. If this is true, then research on this topic has just received another intellectual injection that should be married into our current concept of how the Bivalvia has evolved and radiated as a result, at least in part, by natural selection through predation.

I am aware of the inherent difficulties in undertaking discrete genetic studies upon randomly externally cross-fertilizing bivalves when the sex of the gamete donors cannot often be determined until autopsy. Such research should, however, be a challenge for us, not a hinderance, and that such animals, gregarious, numerous, prolific, and economically important as well as sessile bioindicators of changing environmental regimes should be receiving far more of our attention than they do currently. With the modern technology of DNA fingerprinting before us, research upon the Bivalvia should, already, have seen a quantum leap in output, but it clearly has not. Even DNA technology is unnecessary, however, for some bivalves, which possess self-fertilizing representatives, e.g. the Galeommatoida, and O Foighil (1989) has been able to come to important conclusions regarding the significance of planktotrophy versus direct development in the dispersal of representatives of one cosmopolitan genus of this superfamily, *Lasaea*. But there are many other lineages of hermaphroditic bivalves about which virtually nothing is known, for example, the Anomalodesmata (Morton, 1985).

I recently published a paper (Morton, 1991a) in which I argued that life history tactics and reproductive strategies among a suite of bivalves occupying a freshwater to marine continuum were related to the microhabitats occupied (Table 3). This model will, hopefully, be tested by others. I hesitate to ask this, however, but why is it that the Bivalvia so obviously sessile, so obviously in intimate reality with a sweep of aquatic habitats from mountain pools to the abyss have not become *the* model for such studies and further, since we now know that many of their life history traits can be environmentally regulated, that they also become *the* model to help us understand how such natural and unnatural perturbations

Table 3. The sexual strategies adopted by Hong Kong freshwater, estuarine and intertidal bivalves (After Morton, 1991a).

		Sexual strategy adopted					
	Hermaphroditic: (brooding)	Hermaphroditic/ dioecious: Strongly environmentally regulated sex ratio (brooding)	Dioecious: Pronounced female bias (brooding in <i>Anodonta</i>)	Dioecious: Overall female bias; female bias in juveniles (non-brooding)	Dioecious: Slight overall female bias; male bias in juvenile <i>Brachidontes</i> (non-brooding)	Dioecious: (Alternative sexuality in <i>Saccostrea</i>): Slight overall male bias; male bias in juveniles (non-brooding)	Dioecious Slight male bias (not significant) (non-brooding)
Freshwater (small lotic)	<i>Musculium lacustre</i> <i>Pisidium clarkeanum</i> <i>Pisidium amandalei</i>	<i>Corbicula fluminea</i>					
Freshwater (large lentic)			<i>Anodonta woodiana</i> <i>Limnoperna fortunei</i>				
Freshwater (large lotic)				<i>Corbicula</i> cf. <i>fluminalis</i>			
Mangrove					<i>Polymesoda erosa</i>		
Mangrove					<i>Brachidontes variabilis</i>		
Mangrove						<i>Gafrarium pectinatum</i>	
Harbour						<i>Mytilopsis sallei</i> <i>Saccostrea cucullata</i>	
Intertidal marine							<i>Perna viridis</i> <i>Donax semigranosus</i>

work at the individual, population and species levels.

C. M. Yonge was fascinated by the Bivalvia and laid the foundation for our modern understanding of them. I have read recently the paper by Mikkelsen and Bieler (1989) about the yo-yoing galeommatoidean *Divariscintilla yoyo* Mikkelsen and Bieler. I am also reminded of the work I did upon *Chlamydoconcha orcutti* Dall (Fig. 7A) (Morton, 1981) which is one of the most remarkable of bivalves. It has a minute shell, a weirdly anteriorly monomyarian musculature and very strange defensive appendages. The female also possesses a, possibly parasitic, dwarf male (Fig. 7B). This animal is as exotic as any gastropod. The Galeommatoidea must be one of the most fascinating superfamilies of the Bivalvia. Every study of their numerous representatives speaks of their strange adaptations. Yet, all would agree that the taxonomy and systematics of the group, at every level, are a mess. We desperately need someone to sort them out because I believe that their story is one of the strangest yet to be told. We should

be fascinated by such animals and encourage work upon them for they not only expand our understanding of the full extent of bivalve radiation but also open up new research horizons into the origins, through neoteny, of commensalism and, possibly, parasitism.

Bivalves, alone among the Mollusca, are overwhelmingly economically and ecologically significant and yet they seem, returning to my first figures, to be of declining interest to academic malacologists. Clearly, however, there is not an overall decline in interest (Fig. 3). Is it possible that we as academic malacologists are not in step with globally changing perceptions of the Bivalvia? Is it, further, possible that we are missing a golden harvest of research money and careers that could ultimately be more rewarding? It is clear that few applied aspects of our chosen class were part of this symposium, i.e. their pollution monitoring potential, mariculture significance and their importance as significant fresh water and marine foulers. It could be useful to convene

LITERATURE CITED

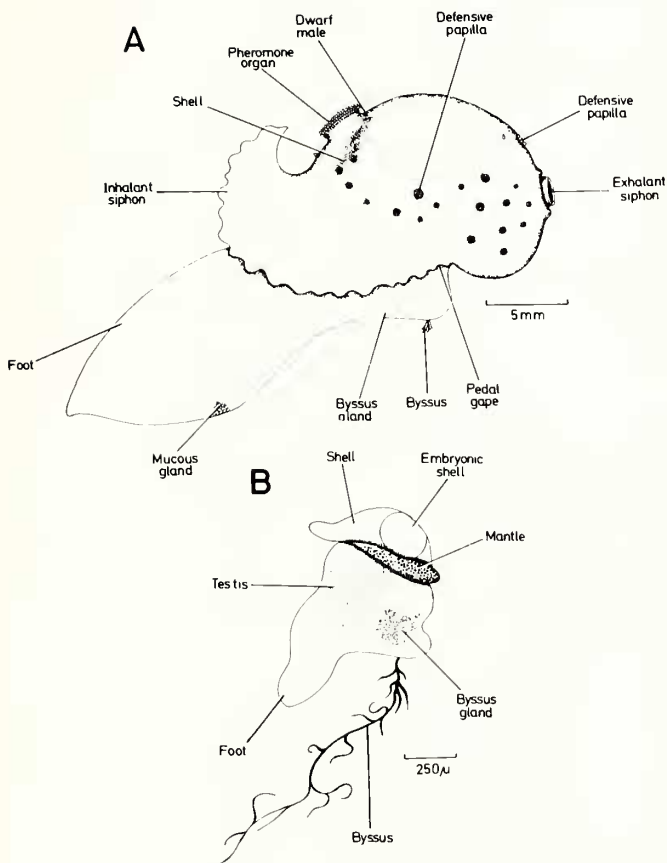


Fig. 7. *Chlamydoconcha orcutti*. A, female; B, dwarf male (after Morton, 1981).

joint meetings of academic and applied bivalve workers on specific topics. I am aware, for example, of the regularly organized pectinid workshops (the 8th was convened in 1991, in Cherbourg, France) that have brought together a rich mix of pure and applied malacologists to great effect. If, therefore, you agree, in any way with my analysis of the current situation with regard to trends and omissions in bivalve research, then perhaps we can persuade the American Malacological Union to assist us in bringing more academic and applied bivalve malacologists together so that the two groups of scientists can begin to benefit, more fully, from the closer cooperation that such meetings would foster.

ACKNOWLEDGMENTS

I am very pleased that Paul Scott and his colleagues seized the initiative in organizing a Symposium and subsequent Workshop on the Bivalvia. I am also grateful to Paul for convening this Symposium and to the Councils of the American Malacological Union and the Western Society of Malacologists for agreeing to host the meeting. I am further grateful that I had the opportunity to address the Opening Session.

- Akberali, H. B. and E. R. Trueman. 1985. Effects of environmental stress on marine bivalve molluscs. *Advances in Marine Biology* 22:101-198.
- Allen, J. A. 1983. The ecology of deep sea molluscs. In: *The Mollusca*. Vol. 6. Ecology. W. D. Russell-Hunter, ed. pp. 29-75. Academic Press, Inc., Orlando, Florida.
- Allen, J. A. and H. L. Sanders. 1969. *Nucinella serrei* Lamy (Bivalvia: Protobranchia), a monomyarian solemyid and possible living actinodont. *Malacologia* 7:381-396.
- Britton, J. C. and B. Morton. 1986. Polymorphism in *Corbicula fluminea* (Bivalvia: Corbiculacea) from North America. *Malacological Review* 19:1-43.
- Cain, A. J. 1988. The colours of marine bivalve shells with special reference to *Macoma balthica*. *Malacologia* 28:289-312.
- Carlton, J. T. 1987. Patterns of transoceanic marine biological invasions in the Pacific Ocean. *Bulletin of Marine Science* 41:452-465.
- Food and Agriculture Organization of the United Nations. 1989. Year book. Fishery Statistics for 1987. Vol. 65. FAO Fisheries Series No. 33. pp. 369.
- Griffiths, C. L. 1990. Spatial gradients in predation pressure and their influence on the dynamics of two littoral bivalve populations. In: *The Bivalvia. Proceedings of a Memorial Symposium in Honour of Sir Charles Maurice Yonge, Edinburgh, 1986*. B. Morton, ed. pp. 321-332. Hong Kong University Press, Hong Kong.
- Harper, E. M. 1991. The role of predation in the evolution of cementation of bivalves. *Palaeontology* 34:455-460.
- Kijviriyi, V., E. S. Upatham, V. Viyanant and D. S. Woodruff. 1991. Genetic studies of Asiatic clams, *Corbicula*, in Thailand: allozymes of 21 nominal species are identified. *American Malacological Bulletin* 8:97-106.
- Knudsen, J. 1979. Deep sea bivalves. In: *Pathways in Malacology*. S. van der Spoel, A. C. van Bruggen and J. Lever, eds. pp. 195-224. Bohn, Scheltema and Holkema, Utrecht.
- Lee, S. Y. 1985. The population dynamics of the green mussel, *Perna viridis* (L.) in Victoria Harbour, Hong Kong - dominance in a polluted environment. *Asian Marine Biology* 2:107-118.
- McMahon, R. F. 1983. Ecology of an invasive pest bivalve, *Corbicula*. In: *The Mollusca*. Vol. 6. Ecology. W. D. Russell-Hunter, ed. pp. 505-561. Academic Press, Inc., Orlando, Florida.
- Mikkelsen, P. M. and R. Bieler. 1989. Biology and comparative anatomy of *Divariscinilla yoyo* and *D. troglodytes*, two new species of Galeomatidae (Bivalvia) from stomatopod burrows in Eastern Florida. *Malacologia* 31:175-195.
- Morton, B. 1981. The biology and functional morphology of *Chlamydoconcha orcutti* Dall with a discussion on the taxonomic status of the Chlamydoconchacea (Mollusca: Bivalvia). *Journal of Zoology, London* 195:81-122.
- Morton, B. 1982. Functional morphology of *Bathyarca pectunculoides* (Bivalvia: Arcoacea) from a deep Norwegian fjord with a discussion of the mantle margin in the Arcoidea. *Sarsia* 67:269-282.
- Morton, B. 1985. Adaptive radiation in the Anomalodesmata. In: *The Mollusca*. Vol 10. Evolution. E. R. Trueman and M. Clarke, eds. pp. 405-459. Academic Press, New York.
- Morton, B. 1987a. Recent marine introductions into Hong Kong. *Bulletin of Marine Science* 41:503-513.
- Morton, B. 1987b. Polymorphism in *Corbicula fluminea* (Bivalvia: Corbiculacea) from Hong Kong. *Malacological Review* 20:105-127.
- Morton, E. (Editor) 1990a. *The Bivalvia. Proceedings of a Memorial Symposium in Honour of Sir Charles Maurice Yonge, Edinburgh, 1986*. Hong Kong University Press, Hong Kong. 355 pp.
- Morton, B. 1990b. Corals and their bivalve borers - the evolution of a symbiosis. In: *The Bivalvia. Proceedings of a Memorial Symposium in*

- Honour of Sir Charles Maurice Yonge, Edinburgh, 1986. B. Morton, ed. pp. 11-46. Hong Kong University Press, Hong Kong.
- Morton, B. 1991a. Do the Bivalvia exhibit environment-specific sexual strategies? A Hong Kong model. *Journal of Zoology, London* 223:131-142.
- Morton, B. 1991b. 'Cockles and mussels - alive, alive O'. Inaugural Lecture. *University of Hong Kong, Supplement to the Gazette*. Vol. XXXVIII. No. 1. pp. 1-20.
- National Academy of Sciences. 1980. *The International Mussel Watch*. National Academy of Sciences, Washington, D.C. 248 pp.
- Newell, N. D. 1965. Classification of the Bivalvia. *American Museum Novitates* No. 2206:1-25.
- O Foighil, D. 1989. Planktotrophic larval development is associated with a restricted geographic range in *Lasaea*, a genus of brooding, hermaphroditic bivalves. *Marine Biology* 103:349-358.
- Pojeta, J. and B. Runnegar. 1976. *Fordilla troyensis* and the earliest history of pelecypod mollusks. *American Science* 62:706-711.
- Purchon, R. D. 1987. Classification and evolution of the Bivalvia: an analytical study. *Philosophical Transactions of the Royal Society, Series B* 316:277-302.
- Reid, R. G. B. and A. M. Reid. 1974. The carnivorous habits of members of the septibranch genus *Cuspidaria* (Mollusca: Bivalvia). *Sarsia* 56:47-56.
- Sanchez-Salazar, M. E., Griffiths, C. L. and R. Seed. 1987a. The interactive roles of predation and tidal elevation in structuring populations of the edible cockle, *Cerastoderma edule*. *Estuarine, Coastal and Shelf Science* 25:245-260.
- Sanchez-Salazar, M. E., Griffiths, C. L. and R. Seed. 1987b. The effect of size and temperature on the predation of cockles *Cerastoderma edule* (L.) by the shore crab *Carinus maenas* (L.) *Journal of Experimental Marine Biology and Ecology* 111:181-193.
- Stanley, S. M. 1973. Effects of competition on rates of evolution, with special reference to bivalve mollusks and mammals. *Systematic Zoology* 22:486-506.
- Stanley, S. M. 1977. Trends, rates and patterns of evolution in the Bivalvia. In: *Patterns of Evolution*. A. Hallam, ed. pp. 209-250. Elsevier, Amsterdam.
- Stanley, S. M. 1986a. Anatomy of a regional mass extinction: Plio-Pleistocene decimation of the western Atlantic bivalve fauna. *Palaios* 1:17-36.
- Stanley, S. M. 1986b. Population size, extinction, and speciation: the fission effect in Neogene Bivalvia. *Paleobiology* 12:89-110.
- Taylor, J. D. 1981. The evolution of predators in the late Cretaceous and their ecological significance. In: *Chance, Change and Challenge: The Evolving Biosphere*. P. L. Forey, ed. pp. 229-240. The British Museum (Natural History), London and Cambridge University Press, Cambridge.
- Tsoi, S. C. M., S. C. Lee, W. L. Wu and B. Morton. 1990. Genetic variation in *Corbicula fluminea* (Bivalvia: Corbiculoidea) from Hong Kong. *Malacological Review* 23:81-90.
- Ventilla, R. F. 1982. The scallop industry in Japan. *Advances in Marine Biology* 20:309-382.
- Ventilla, R. F. 1984. Recent developments in the Japanese oyster culture industry. *Advances in Marine Biology* 21:1-57.
- Vermeij, G. 1977. The Mesozoic marine evolution: evidence from snails, predators and grazers. *Paleobiology* 3:245-258.
- Vermeij, G. 1989a. Geographical restriction as a guide to the causes of extinction: the case of the cold northern oceans during the Neogene. *Paleobiology* 15:335-356.
- Vermeij, G. 1989b. Invasion and extinction: the last three million years of North Sea pelecypod history. *Conservation Biology* 3:274-281.
- Waller, T. R. 1971. The glass scallop *Propeamussium*, a living relict of the past. *Report of the American Malacological Union Pacific Division* 1970:5-7.
- Willan, R. C. 1987. The mussel *Musculista senhousia* in Australasia, another aggressive alien highlights the need for quarantine at ports. *Bulletin of Marine Science* 41:475-489.
- Yonge, C. M. 1928. Structure and function of the organs of feeding and digestion in the septibranchs, *Cuspidaria* and *Poromya*. *Philosophical Transactions of the Royal Society of London, Series B* 216:221-263.
- Yonge, C. M. and T. E. Thompson (Editors). 1978. Evolutionary systematics of bivalve molluscs. *Philosophical Transactions of the Royal Society of London, Series B* 284:199-436.

Date of manuscript acceptance: 25 November 1991